Predicting White-Tailed Deer Habitat Use in Northern Idaho
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P. R. Krausman and N. S. Smith, eds. Deer in the southwest: a symposium. School Renewable Nat. Resour., Univ. Arizona, Tucson.

MONTGOMERY, G. G. 1963. Nocturnal movements and activity rhythms of white-tailed deer. J. Wildl. Manage. 27:422–427.

NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541–545.

OCKENFELS, R. A., AND J. A. BISSONETTE. 1982. Estimate of white-tailed deer activity levels in Oklahoma. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies. 36:445–453.

RAUTENSTRAUCH, K. R. 1987. Ecology of desert mule deer in southwest Arizona. Ph.D. Diss., Univ. Arizona, Tucson. 37pp.

———, AND P. R. KRAUSMAN. 1989. Influence of water availability on movements of desert mule deer. J. Mammal. 70:197–201.

ROBINETTE, W. L. 1966. Mule deer home range and dispersal in Utah. J. Wildl. Manage. 30:335–349.

SOUTHWOOD, T. E. 1966. Ecological methods. Methuen, London, U.K. 524pp.

TABER, R. D., AND R. F. DASMANN. 1958. The black-tailed deer of the chaparral. Its life history and management in the North Coast Range of California. Calif. Dep. Fish and Game, Game Bull. 8. 163pp.

TRUETT, J. C. 1972. Ecology of desert mule deer, *Odocoileus hemionus crooki* Mearns, in southeast Arizona. Ph.D. Diss., Univ. Arizona, Tucson. 64pp.

VOGEL, W. O. 1989. Response of deer to density and distribution of housing in Montana. Wildl. Soc. Bull. 17:406–413.

WALLMO, O. C. 1981. Mule and black-tailed deer distribution and habitats. Pages 1–25 *in* O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., San Diego, Calif. 383pp.

WOOD, A. K., R. J. MACKIE, AND K. L. HAMLIN. 1989. Ecology of sympatric populations of mule deer and white-tailed deer in a prairie environment. Mont. Dep. Fish, Wildl. and Parks. 97pp.

ZAR, J. H. 1974. Biostatistical analysis. Prentice Hall, Inc., Englewood Cliffs, N.J. 620pp.

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PREDICTING WHITE-TAILED DEER HABITAT USE IN NORTHERN IDAHO

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Abstract: Winter habitat use patterns of white-tailed deer (*Odocoileus virginianus*) have been studied extensively across their northern distribution. However, previous research has contributed little to predicting habitat use of unstudied populations. Thus, we evaluated winter habitat use of white-tailed deer in the Priest River drainage of northern Idaho and developed a predictive model of winter habitat selection. Our findings suggest that winter habitat selection is predictable given seasonal changes in basal metabolism and the effects of snow accumulation on forage availability and energy expenditure. During early (18 Nov–8 Jan) and late (3 Mar–2 Apr) winter, when basal metabolic rates were elevated and snow depths did not exceed 30 cm, white-tailed deer selected lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) pole timber stands that provided the greatest availability of preferred forage species. During mid-winter (9 Jan–2 Mar) when snow depths exceeded 40 cm and basal metabolism was depressed, white-tailed deer selected western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) old growth forest stands characterized by depauperate understories, dense canopy cover, and low snow accumulation. We analyzed this relationship with logistic regression, which provided a biologically meaningful model of winter habitat selection that could be applied to predict habitat selection patterns of unstudied populations. Our data suggest that in northern Idaho and on other white-tailed deer winter ranges where snow depths commonly exceed 40 cm, habitat managers should provide old growth forest, or mature second growth stands with similar structural attributes to satisfy winter habitat requirements.

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In the northern coniferous forested portions of their geographical distribution, white-tailed deer use a wide variety of habitats. During snow-free periods, habitat use is dependent upon the presence of digestible forage. During periods of snow cover, deer assume an energy conservation mode and use closed-canopied forests (Moen

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1978). This pattern of habitat use occurs across the northern range of the species in New Brunswick (Telfer 1970, Drolet 1976), New York (Cook and Hamilton 1942), Maine (Banasiak 1961), Michigan (Ozoga and Gysel 1972, Beier and McCullough 1990), Minnesota (Wetzel et al. 1975), Montana (Martinka 1968, Singer 1979, Mundinger 1980, Dusek et al. 1989), and Idaho (Keay and Peek 1980, Owens 1981). Those investigations represent descriptive case histories, however, and do not predict habitat use on the basis of environmental variables. Predictions may enhance planning for habitat retention in managed forests, and provide a basis for integrating habitat management for the entire wildlife complex as well.

Snow cover is a major influence on deer habitat use in northern ranges (Moen 1978, Parker et al. 1984). We investigated the hypothesis that snow cover can be used to predict winter habitat selection, and we provide a model that can be used to predict deer habitat use using snow depth. An assessment of factors influencing deer habitat selection is included. We used multivariate comparisons of seasonal habitat use patterns to identify optimum combinations of habitat components during each winter period.

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STUDY AREA

The study area included the northern half of the Priest River drainage in northern Idaho and northwestern Washington. The drainage extends from north to south with elevations ranging from 700 m in the valley at the southern end of the winter range to peaks in the Selkirk Mountains exceeding 2,100 m. The western hemlock and western red cedar habitat type series prevail on low elevation (<1,500 m) white-tailed deer habitat, whereas the subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) habitat type series dominate high elevation communities (Cooper et al. 1987). The Douglas-fir/ninebark (*Physocarpus malvaceus*) habitat type commonly occurs on southerly exposures in the southern portion of the drainage. Douglas-fir, grand fir (*Abies grandis*), lodgepole pine, western larch (*Larix occidentalis*), and western white pine (*Pinus monticola*) occur in seral stands. Communities in the Priest River drainage are characterized by lush understories dominated by shrub species including pachistima (*Pachistima myrsinites*), Oregon grape (*Berberis repens*), blue huckleberry (*Vaccinium globulare*), Sitka alder (*Alnus sinuata*), common snowberry (*Symphoricarpos albus*), Scouler willow (*Salix scouleriana*), serviceberry (*Amelanchier alnifolia*), and various roses (*Rosa* spp.). Queen cup beadlily (*Clintonia uniflora*), wild ginger (*Asarum caudatum*), wild sarsaparilla (*Aralia nudicaulis*), laceflower (*Tiarella trifoliata*), strawberries (*Fragaria* spp.), pinegrass (*Calamagrostis rubescens*), and orchard grass (*Dactylis glomerata*) are common herbaceous species. Plant nomenclature followed Hitchcock and Cronquist (1973).

Wildfire was the most important natural disturbance in the area and burned over much of the district in the early part of the century (U.S. For. Serv. records, Priest River Ranger Dist., Priest River, Id.). Now, timber harvest is the primary factor influencing white-tailed deer habitat. The Priest River climate is transitional between northern Pacific coastal and continental weather patterns resulting in wet conditions during winter and spring, and dry summers. Annual precipitation averages 83 cm in the valley with close to 60% of the precipitation falling from November to March in the form of snow. Snow cover usually persists on the valley floor from early December through the end of March. Monthly temperatures in the valley range from a mean minimum in January of −8.1 C and maximum of −1.1 C to a mean minimum of 8.3 C and maximum of 28.4 C in July (Finklin 1983).

METHODS

Deer were captured during the winters of 1986–87 and 1987–88 in Clover traps baited with alfalfa (Clover 1956). Each deer was fitted with a mortality sensitive, 0.5-kg radio collar (Telonics Inc., Mesa, Ariz.). Fawn collars were adjusted to adult size and fitted to the animal following Craighead et al. (1969). Habitat use was determined from vegetation structure, composition, and topographic characteristics measured at radio locations obtained throughout the year. We relocated each study animal from the ground every 5–10 days. Eighty-seven percent of the radio locations were obtained during crepuscular and daytime periods. Because of the rugged, dissected features of the Priest Lake area, triangulation was inadequate to establish accurate locations. Alternatively, each deer was relocated by approaching to within a distance of 100–200 m and circling until an accurate location could be isolated to a uniform stand of vegetation. The procedure was efficient and seldom resulted in displacement of the deer. We subsequently revisited a subset of the locations to analyze habitat characteristics. Each site was examined for recent deer sign that represented the center of a 15-m diameter plot. The size plot was selected to reflect the range of immediate environmental effects to which a white-tailed deer would respond.

Topographic variables included elevation, percent slope, and the product of the cosine of the aspect (azimuth) and the slope (%), scaled from northeast to southwest, which more effectively represented the effect of aspect on the environment (Stage 1976). We measured overstory characteristics including the average diameter at breast height (dbh), canopy closure (densiometer), basal area (20 BAF prism), canopy height (clinometer), the densities of saplings and mature trees of each species (point center quarter method), the habitat type (Cooper et al. 1987), and the stand age by boring 1–3 trees representing the largest, prevalent age class. Cover of understory species was determined with a line point transect (Levy and Madden 1933), and we recorded the height of a representative shrub of each species. Additionally, hiding cover of the site was measured with a cover pole following Griffith and Youtie (1988).

We evaluated the marginal distributions of the variables for univariate normality. Many understory and tree species were infrequent in sample plots and poorly distributed, and therefore eliminated from further analysis. Sapling densities were transformed with either the square root or log transformations, and all percentage data except canopy closure were transformed with the arcsine square root transformation.

We identified 6 seasons that reflected distinct periods of habitat use. The seasons including spring (3 Apr–25 May), summer (26 May–28 Aug), autumn (29 Aug–17 Nov), early winter (18 Nov–8 Jan), mid-winter (9 Jan–2 Mar), and late winter (3 Mar–2 Apr). Each sample plot was assigned to the appropriate season for analysis.

Initially, differences in habitat use among the 6 seasons were tested with a multivariate analysis of variance using Roy's greatest root test criteria, and pairwise comparisons with Hotelling's T^2 (Johnson and Wichern 1988). That was analogous to performing an overall analysis of variance followed by Fisher's protected least significant difference tests in the univariate case. Our null hypothesis was that the mean vectors of the individual seasons did not differ. Seasons that were not significantly different were combined for further analysis.

We used canonical analysis to identify the variables that summarized the variation among seasons (Raphael 1981). The analysis was conducted on each season against the remaining combined observations to reveal the combination of variables unique to each season that characterized habitat selection. Similar multivariate approaches successfully segregated species-specific (Cavallaro et al. 1981, Folse 1981) and season-specific (Boyce 1981) habitat selection.

The eigenvectors of the product of the treatment (season) variance-covariance matrix and the inverse of the error variance-covariance matrix are the columns of canonical coefficients (Johnson and Wichern 1988). The number of eigenvectors is equal to the minimum of 1 less than the number of groups or the number of variables. Our analysis produced 1 eigenvector, because there were 2 groups (1 season and the other seasons in combination). The canonical variate is the product of the eigenvector and the variables, and is the linear combination of the variables that will maximize the Mahalanobis distance among seasons, thus producing the greatest separation or contrast of seasonal habitat use. In our analysis, the correlations of the variables with the canonical variates were interpreted rather than the canonical coefficients, because the correlations are more stable (Raphael 1981; Williams 1981, 1983). We assumed the variables with larger correlations provided the most meaningful description of seasonal use, although the sign of all variable correlations was used to detect selection gradients in the canonical structure.

We examined selection of habitat categories during winter with univariate analysis. Stand type was categorized as old growth ($\geq$50 cm dbh and ≥160 yr old), mature timber (>23 cm dbh), pole timber (>7.5 cm dbh and <23 cm dbh), or unforested (<30% canopy closure). Aspect was defined as northeast (315°–360°, or 0°–135°) or southwest (135°–315°). Percent slope was combined into 3 categories: 0–25%, 26–50%, and >51%. The available area was defined by a composite 95% harmonic mean home-range contour calculated from the locations of all deer (Dixon and Chapman 1980). We used locations obtained during the 3 winter periods to calculate the area boundary, and we considered habitat components within the area equally available to all deer throughout winter.

We used the Chi-square goodness-of-fit test to evaluate the null hypothesis that the use of habitat categories equalled availability after Neu et al. (1974) and Byers et al. (1984). All expected values exceeded 5.00 (Roscoe and Byars 1971). Chi-square values from tests with 2 categories were adjusted with the Yates' correction for continuity (Zar 1984).

We measured snow characteristics weekly during winter along 6 transects situated in sites representative of mature timber, pole timber, and clearcuts on the winter range. We measured snow depth and estimated deer sinking depth with a gauge calibrated to 1,900 g/cm^2 to imitate a standing or walking white-tailed deer (Hepburn 1978). Two transects were located at a representative site in 2 separate stands, in each stand type, on level ground. The transects were read weekly in the same order, alternating among stand types, beginning at a different transect each week.

We analyzed the relationship of snow accumulation to deer use of stand types with logistic regression using the maximum likelihood procedure (SAS Inst. Inc. 1987). The trichotomous classification of deer observations into stand types was treated as the dependent variable, whereas snow depth and sinking depth measures in pole timber, mature timber, and clearcuts formed the independent variables. The individual snow characteristics were used to develop a model to predict the probability of deer use of old growth, mature timber, and pole timber stands. We determined suitability of the model with a Chi-square goodness-of-fit test under the null hypothesis that the data may be appropriately modelled with logistic regression (SAS Inst. Inc. 1987). Non-significance ($P > 0.25$) suggested the model was suitable (Hosmer and Lemeshow 1989). We tested independent variable effects with a Wald Chi-square statistic (Hosmer and Lemeshow 1989). Individual coefficients were analyzed with a t-test.

RESULTS

From 23 May 1987 to 10 December 1988, we obtained 875 relocations for 17 radio-collared deer, and we selected 590 for habitat analysis including 219 winter locations. Habitat use patterns differed ($F = 38.72$, $P < 0.001$) among seasons overall, but pairwise comparisons revealed that use did not differ during early and late winter ($T^2 = 2.52$, $P = 0.401$). Therefore, we combined early and late winter observations for further analysis. Otherwise, habitat use differed ($P < 0.001$) among the remaining seasons including the combination of early and late winter observations.

Early and Late Winter

During early and late winter, the study animals used similar habitats. Seventy-three percent of observed use occurred in pole and mature timber on the gently sloping valley floor, while 23% of use occurred in mature Douglas-fir stands on the adjacent slopes. Canonical analysis defined early winter and late winter habitat as forested stands that were moderately stocked with relatively tall (24 m canopy height), closed (74% canopy cover) canopies (Table 1). Both Douglas-fir and lodgepole pine dominated pole timber stands on the valley floor and were important variables in early and late winter habitat selection. Mature stands on south and west facing exposures were on Douglas-fir/ninebark habitat types and stocked almost exclusively with Douglas-fir. The infrequent occurrence of western hemlock regeneration and dominance of Douglas-fir regeneration emphasized the importance of dry forest habitat types. In addition, both pole timber stands and mature second growth on southerly exposures were characterized by dense deciduous and evergreen shrub cover (Fig. 1). Oregon grape was important both as a forage species (Pauley 1990) and a discriminating variable. The deer selected sites with gentle slopes at low elevations (Table 1).

Mid-Winter

During mid-winter, 61% of the observed habitat use occurred in old-growth western red cedar and western hemlock stands along the river

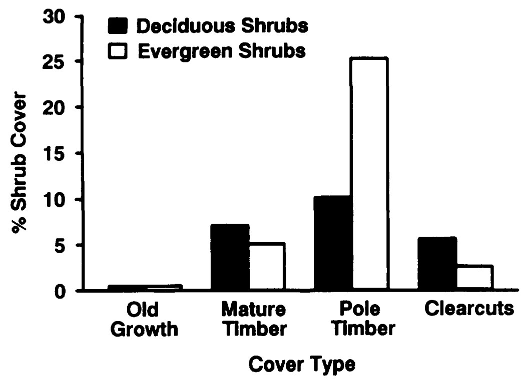

Fig. 1. Cover (%) of deciduous and evergreen shrubs in 4 stand types in the Priest River drainage of northern Idaho, 1987–88.

bottom, whereas 14% of the observations were in mature second growth along the river. Nineteen percent of the observed use occurred in mature second growth on south and west facing slopes. Canonical analysis characterized mid-winter habitat as forested stands that were, on average, exceptionally old (238 yr), tall (31 m), closed-canopied (87% canopy cover), and densely stocked (49 m^2/ha basal area) with mature western red cedar and western hemlock, which prevailed in river bottom old growth stands (Table 1). The abundance of mature cedar and hemlock emphasized the importance of climax forest during mid-winter. Mature forests used during mid-winter had depauperate understories (Fig. 1). However, trillium (*Trillium ovatum*), ladyfern (*Athyrium filix-femina*), and oak fern (*Gymnocarpium dryopteris*) were prevalent on sites used during mid-winter and were identified as important variables. These forbs are indicators of the mesic western red cedar/wild ginger and western hemlock/queen cup beadlily habitat types used along the river during mid-winter. Additionally, canonical analysis

Table 1. Variables defining white-tailed deer winter habitat use in the Priest River Drainage of northern Idaho, 1987–88.

Variable[a]	Spring, summer, autumn	Early winter	Mid-winter	Late winter
Overstory structure				
Mean dbh (cm)	20		35	
Canopy height (m)	21	24	31	25
Canopy cover (%)	66	74	87	74
Basal area (m^2/ha)	28		49	
Stand age (yr)	102		238	
Mature tree density (trees/ha)				
Western red cedar	75	64	181	27
Western hemlock	65		156	
Douglas-fir	133	143		259
Lodgepole pine	172	319		242
Total mature tree density	535	694		650
Sapling density (trees/ha)				
Western hemlock	121	84		55
Douglas-fir	196	249		290
Shrub cover (%)				
Oregon grape	0.8	1.1		2.2
Total shrub cover	25		6	
Shrub height (cm)	76		37	
Herbaceous cover (%)				
Ladyfern and oak fern[b]	0.7		1.5	
Trillium	0.1		0.4	
Total herbaceous cover	13		6	
Topography				
Elevation (m)	797	759	762	778
Slope (%)[c]	10	5		9
Aspect (% use)				
Northeast	26		7	
Southwest	74		93	

[a] Means are presented for those variables selected with canonical analysis during the respective winter period.
[b] The canopy coverages of ladyfern and oak fern were combined for analysis.
[c] Aspect and slope (%) were combined and transformed for the actual analysis following Stage (1976).

identified the importance of low elevation sites and southwesterly exposures (Table 1).

Univariate analysis confirmed our interpretation of the canonical variates and further characterized winter habitat selection. White-tailed deer use of stand types (mid-winter $\chi^2 = 378.62$, $P < 0.001$; early/late winter $\chi^2 = 15.36$, $P = 0.002$) and aspects (mid-winter, $\chi^2 = 4.75$, $P = 0.029$; early/late winter, $\chi^2 = 3.906$, $P = 0.048$) differed from availability throughout winter, whereas use of slope categories differed only during early and late winter (mid-winter $\chi^2 = 1.609$, $P = 0.447$; early/late winter $\chi^2 = 6.932$, $P = 0.031$).

Throughout winter, deer avoided openings and used mature second growth in proportion to its occurrence (Fig. 2). Pole timber was selected during early and late winter but strongly avoided during mid-winter when deer selected old growth, which was used proportionately during early and late winter. Priest Lake white-tailed deer selected south and west facing exposures throughout winter and gently sloping terrain during early and late winter (Fig. 2). Lack of selection of slope categories during mid-winter was related to increased use of steeply sloping, south and west facing aspects during this period.

White-tailed deer use of warm exposures was partially related to weather patterns. Southerly aspects were used an average of 5.56 days (SE = 0.41) after the most recent snow storm, whereas the duration between storms averaged only 2.21 days (SE = 0.32), suggesting warm exposures were used primarily during melt periods because of increased snow melt and insolation.

Habitat Use and Snow Accumulation

Logistic regression analysis of snow depth and stand type use provided a biologically meaningful model of the response of white-tailed deer to snow accumulation. The snow depth measurements provided the best model fit, whereas predictions with sinking depths were generally poor ($P < 0.201$). Furthermore, predictions from snow depths in forested types were better than those from the depth of snow in clearcuts (clearcut depth $\chi^2 = 72.30$, $P = 0.278$; pole timber depth $\chi^2 = 72.20$, $P = 0.537$; mature timber depth $\chi^2 = 70.43$, $P = 0.596$). We used only snow depth measures to predict use because of the poor fit of sinking depth models, and because the depth measures were easier to replicate. The effects of the snow depths were significant ($P <$

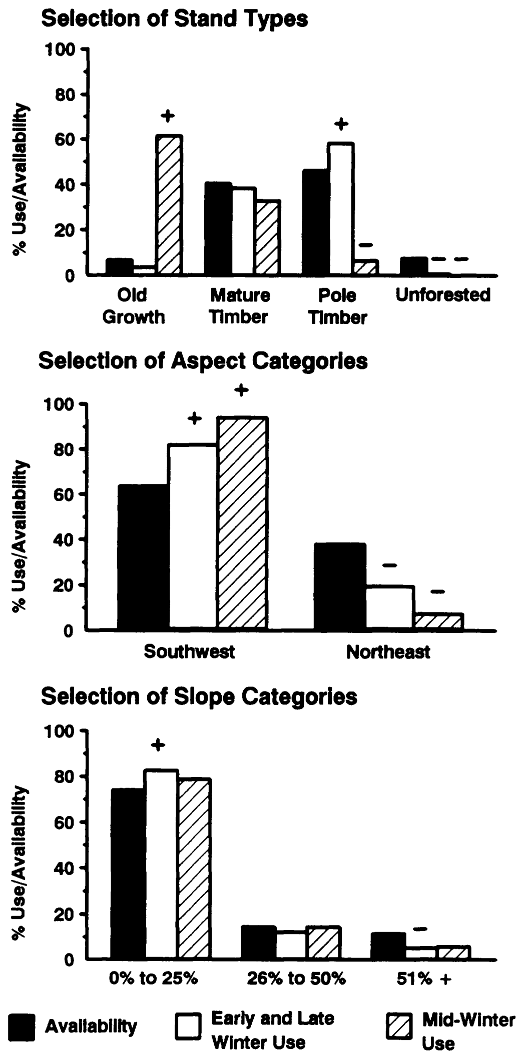

Fig. 2. Winter selection of stand type, aspect, and slope categories by white-tailed deer in the Priest River Drainage of northern Idaho, 1987–88. A plus indicates preference, and a minus indicates avoidance ($P < 0.05$).

0.001) and the individual coefficients differed from zero ($P < 0.0025$).

The probability of white-tailed deer use of each stand type was predicted by the logistic functions,

$$P\ (\text{Pole Timber Use}) = \frac{1}{1 + e^{(g1)} + e^{(g2)}}$$

$$P\ (\text{Mature Timber}) = \frac{e^{(g2)}}{1 + e^{(g1)} + e^{(g2)}}$$

$$P\ (\text{Old Growth Use}) = \frac{e^{(g1)}}{1 + e^{(g1)} + e^{(g2)}}$$

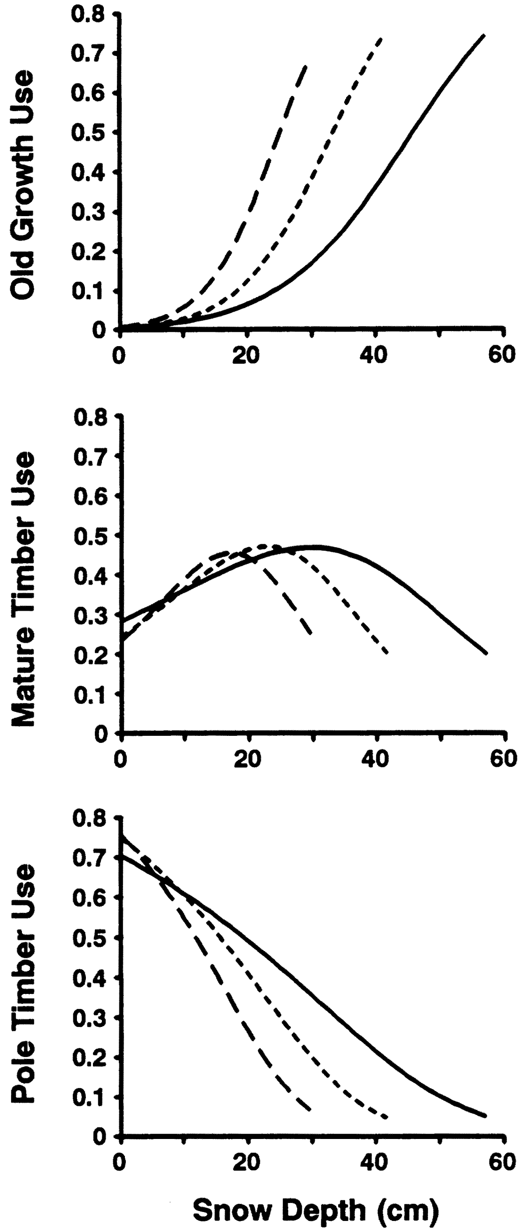

Fig. 3. White-tailed deer use of stand types predicted with logistic regression from snow depths in clearcuts (solid line), pole timber (dotted line), and mature timber (dashed line) in northern Idaho, 1987–88.

where e = the base of the natural logarithm, and where the snow depth (cm) in clearcuts = x, and,

$$g1 = 0.1244(x) - 4.4608$$
$$g2 = 0.0394(x) - 0.9001$$

or where the snow depth in pole timber = x, and,

$$g1 = 0.1832(x) - 4.8394$$
$$g2 = 0.0623(x) - 1.1135$$

or where the snow depth in mature timber = x, and,

$$g1 = 0.2307(x) - 4.5215$$
$$g2 = 0.0842(x) - 1.1660$$

The 3 snow depth measures were highly correlated, and essentially produced the same model except that curves fitted for snow data from more open-canopied types were more gently sloping and shifted to the right (Fig. 3). For example, the probability curves produced by the clearcut snow depths were more gently sloping and shifted to the right of those produced by the depth of snow in pole timber, and likewise for the pole timber snow depth model versus the mature timber snow depth model. The differences were a product of more rapid snow accumulation and snow melt in habitats with more open canopies.

DISCUSSION

Winter habitat selection of white-tailed deer can be explained and predicted in the context of their energy budget. Seasonal metabolic patterns and the effects of snow on forage availability and energy expenditure appear to predispose white-tailed deer to a predictable pattern of habitat selection in northern Idaho.

During early and late winter, white-tailed deer strongly selected for lodgepole pine and Douglas-fir pole timber stands that furnished little canopy cover or snow interception relative to mature forest stands, but provided the greatest abundance of preferred forage including nutritious, evergreen shrub species (Pauley 1990). Snow depths during early and late winter, which were <30 cm, did not greatly reduce forage availability or hinder animal movement (Telfer 1970, Kelsall and Prescott 1971, Mattfield 1974, Drolet 1976, Parker et al. 1984). Although their findings were questioned (Mautz et al. 1992), the work of Hoffman and Robinson (1966), Silver et al. (1969), and Seal et al. (1972) suggested that metabolic activity is high during early and late winter, and there is a corresponding high demand for forage (Ozoga and Verme 1970). During early and late winter, white-tailed deer should choose habitats with moderate to high quantities of preferred forage somewhat irrespective of terrain and canopy cover, except to the extent that these factors affect forage availability.

During mid-winter, white-tailed deer avoided openings and early successional forest stands and selected advanced forest age classes that had relatively little forage but provided the most optimum snow conditions. White-tailed deer were strongly selective of western red cedar and western hemlock old growth forest stands characterized by depauperate understories, dense canopy cover, and low snow accumulation. The change in habitat use from early winter to mid-winter essentially represented a transition from more energy-rich habitats to habitats that allowed efficient energy conservation.

During mid-winter, snow accumulations, which exceeded 40 cm, reduced forage availability, hindered movement, and elevated the energy costs of travel (Mattfield 1974, Parker et al. 1984). These conditions in combination with a depressed basal metabolism and forage intake (Hoffman and Robinson 1966, Silver et al. 1969, Ozoga and Verme 1970, and Seal et al. 1972, cf Mautz et al. 1992), predisposed white-tailed deer to conserve energy by selecting habitats with the least snow to minimize energy expenditure. Mature conifer stands have less snow accumulation (Bloom 1978, Kirchhoff and Schoen 1987) and more stable and less hazardous snow conditions (Verme 1965, Bloom 1978). During mid-winter, deer should choose habitats that maximize energy conservation, somewhat irrespective of forage availability.

The logistic regression analysis revealed a biologically meaningful model of the continuous transition of cover type use in response to snow conditions. The model essentially mirrored the snow depth/energy expenditure relationship presented by Parker et al. (1984), suggesting that deer were acutely responsive to changes in energy expenditure caused by accumulating snow.

Priest River white-tailed deer also selected topographic features in an apparently optimal manner. During periods of snow accumulation, the deer selected gently sloping terrain that minimized energy loss during movement (Moen 1976, Parker et al. 1984). During melt periods, white-tailed deer selected steep, south- and west-facing slopes that had little snow and more insolation than other sites. This overall pattern of use was most evident during mid-winter when snow conditions were most severe.

The entire northern distribution of white-tailed deer, and particularly the coniferous forests in the northern Rockies, encompasses a wide variety of habitats, and white-tailed deer habitat-use patterns vary accordingly. White-tailed deer winter in shrub communities (Martinka 1968, Bell 1988) and in ponderosa pine (Bell 1988), Douglas-fir (Singer 1979, Keay and Peek 1980, Mundinger 1980, Woods 1984, Jenkins and Wright 1988), Englemann spruce (Singer 1979, Mundinger 1980, Jenkins and Wright 1988), and western red cedar (Owens 1981) forest habitats. In addition, white-tailed deer used forests ranging in age from mature second growth to old growth. Selection of topographic features included both southerly (Singer 1979, Keay and Peek 1980, Woods 1984) and northerly exposures (Bell 1988, Berner et al. 1988, Brockman 1988), and both gentle (Mundinger 1980, Jenkins and Wright 1988) and steeply sloping terrain (Woods 1984, Jenkins and Wright 1988). Selection of specific habitats often varied substantially during the course of a winter and among winters of varying severity.

The disparity of findings suggests that studies from 1 area cannot be applied across the species' geographical distribution. However, the variability in habitat selection patterns can be explained by corresponding differences in snow accumulation and habitat characteristics. Collectively, considered in this context, the findings become meaningful and support our model of winter habitat selection.

Where snow conditions caused significant energy expenditure, white-tailed deer selected mature conifer cover including climax old growth forest (Mundinger 1980, Woods 1984, Jenkins and Wright 1988), or mature second growth where old growth was not available (Keay and Peek 1980, Owens 1981, Berner et al. 1988, Brockman 1988). Deer typically selected the oldest available age class of conifer cover characterized by tall, close canopies (>80% canopy cover) and high basal areas of large trees (Woods 1984, Berner et al. 1988, Brockman 1988, Jenkins and Wright 1988). White-tailed deer apparently selected mature conifer cover for structural characteristics to mitigate for snow accumulation, regardless of vegetation association, and somewhat irrespective of forage availability (Owens 1981, Woods 1984, Jenkins and Wright 1988). Conversely, during periods of mild weather and moderate snow conditions, or where winters were less severe, white-tailed deer selected more open-canopied habitats with more optimum forage conditions (Martinka 1968, Mundinger 1980, Woods 1984, Bell 1988, Jenkins and Wright 1988).

Use of topographic features also appears to fit our model of winter habitat selection. White-tailed deer typically used moderate to steeply sloping south and west aspects; this was likely a function of the advantages of enhanced insolation. In northwestern Montana, deer selected northerly aspects, evidently to avoid non-forested habitats on south facing slopes (Berner et al. 1988, Brockman 1988). In the presence of severe winter conditions, when the advantages of warm exposures are diminished, use of gently sloping bottoms was more prevalent (Singer 1979, Mundinger 1980, Jenkins and Wright 1988).

Although our interpretations of previous work represent a posteriori explanations of events based on limited knowledge of the circumstances surrounding the individual studies, winter habitat selection does appear to follow a common theme. In the northern extent of their geographical distribution, white-tailed deer are predisposed to select habitats in a predictable manner in response to the chronology of basal metabolism and the effects of snow on forage availability and energy expenditure. Our findings, as well as the findings of previous work, appear to conform to this model of winter habitat selection.

MANAGEMENT IMPLICATIONS

In northern Idaho and on other white-tailed deer winter habitats where snow depths commonly exceed 40 cm, habitat managers should provide old growth forest, or mature second growth stands with similar canopy structure, to satisfy mid-winter habitat requirements. Habitats providing an abundance of preferred forage are important throughout winter on ranges with little snow accumulation and elsewhere during early and late winter. Preferred winter habitat should be situated at low elevations in gently sloping bottoms and on moderate to steeply sloping south and west facing slopes. The emphasis placed on providing each type of habitat will largely depend on the level of snow accumulation. We suggest using our model as an initial guideline.

LITERATURE CITED

BANASIAK, C. F. 1961. Deer in Maine. Maine Dep. of Inland Fish. and Game, Game Div. Bull. 6, Augusta. 159pp.

BEIER, P., AND D. R. MCCULLOUGH. 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildl. Monogr. 109. 51pp.

BELL, J. H. 1988. Habitat use, movements, and home range of white-tailed deer in the Umatilla River drainage, northeast Oregon. M.S. Thesis, Univ. of Idaho, Moscow. 108pp.

BERNER, K. L., C. E. FIEDLER, AND D. H. PLETSCHER. 1988. White-tailed deer winter habitat use in western Montana second growth forests. Mont. For. and Conserv. Exp. Stn. Res. Rep. No. 2, Univ. of Mont., Missoula. 7pp.

BLOOM, A. M. 1978. Sitka black-tailed deer winter range in the Kadashan Bay area, southeast Alaska. J. Wildl. Manage. 42:108–112.

BOYCE, M. S. 1981. Robust canonical correlation of sage grouse habitat. Pages 152–159 *in* D. E. Capen, ed. The use of multivariate statistics in the studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87.

BROCKMAN, S. P. 1988. Winter habitat selection by the sexes of white-tailed deer. M.S. Thesis, Univ. of Montana, Missoula. 102pp.

BYERS, C. R., R. K. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48:1050–1053.

CAVALLARO, J. I., J. W. MENKE, AND W. A. WILLIAMS. 1981. Use of discriminant analysis and other statistical methods in analyzing microhabitat utilization of dusky-footed woodrats. Pages 222–231 *in* D. E. Capen, ed. The use of multivariate statistics in the studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87.

CLOVER, M. R. 1956. Single-gate deer trap. Calif. Fish and Game 40:367–373.

COOK, D. B., AND W. J. HAMILTON. 1942. Winter habits of white-tailed deer in central New York. J. Wildl. Manage. 6:287–291.

COOPER, S. V., K. E. NEIMAN, R. S. STEELE, AND D. W. ROBERTS. 1987. Forest habitat types of northern Idaho: a second approximation. U.S. For. Serv. Gen. Tech. Rep. INT-236. 135pp.

CRAIGHEAD, J. J., M. G. HORNOCKER, M. W. SHOESMITH, AND R. I. ELLIS. 1969. A marking technique for elk. J. Wildl. Manage. 33:906–909.

DIXON, K. R., AND J. A. CHAPMAN. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040–1044.

DROLET, C. A. 1976. Distribution and movements of white-tailed deer in southern New Brunswick in relation to environmental factors. Can. Field-Nat. 90:123–136.

DUSEK, G. L., R. J. MACKIE, J. D. HERRIGES, JR., AND B. B. COMPTON. 1989. Population ecology of white-tailed deer along the lower Yellowstone River. Wildl. Monogr. 104. 68pp.

FINKLIN, A. L. 1983. Climate of Priest River Experimental Forest, northern Idaho. U.S. For. Serv. Gen. Tech. Rep. RM-159. 53pp.

FOLSE, L. J. 1981. Ecological relationships of grassland birds to habitat and food supply in east Africa. Pages 160–166 *in* D. E. Capen, ed. The use of multivariate statistics in the studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87.

GRIFFITH, B., AND B. A. YOUTIE. 1988. Two devices for estimating foliage density and deer hiding cover. Wildl. Soc. Bull. 16:206–209.

HEPBURN, R. L. 1978. A snow penetration gauge for studies of white-tailed deer and other northern mammals. J. Wildl. Manage. 42:663–667.

HITCHCOCK, C. L., AND A. CRONQUIST. 1973. Flora of the Pacific Northwest. Univ. of Washington Press, Seattle. 730pp.

HOFFMAN, R. A., AND P. F. ROBINSON. 1966. Changes in some endocrine glands of white-tailed deer as affected by season, sex, and age. J. Mammal. 20:206–215.

HOSMER, D. W., AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley and Sons, Inc., New York, N.Y. 307pp.

JENKINS, K. J., AND R. G. WRIGHT. 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. J. Appl. Ecol. 25: 11–24.

JOHNSON, R. A., AND D. W. WICHERN. 1988. Applied multivariate statistical analysis. Second ed. Prentice-Hall Publ., Englewood Cliffs, N.J. 607pp.

KEAY, J. A., AND J. M. PEEK. 1980. Relationship between fires and winter habitat of deer in Idaho. J. Wildl. Manage. 44:372–380.

KELSALL, J. P., AND W. PRESCOTT. 1971. Moose and deer behavior in snow. Can. Wildl. Serv. Rep. Ser. No. 15. 27pp.

KIRCHHOFF, M. D., AND J. W. SCHOEN. 1987. Forest cover and snow: implications for deer habitat in southeast Alaska. J. Wildl. Manage. 51:28–33.

LEVY, E. B., AND E. A. MADDEN. 1933. The point method of pasture analysis. N.Z. J. Agric. 46:267–279.

MARTINKA, C. J. 1968. Habitat relationships of white-tailed and mule deer in northern Montana. J. Wildl. Manage. 32:558–565.

MATTFIELD, G. F. 1974. The energetics of winter foraging by white-tailed deer: a perspective on winter concentration. Ph.D. Diss., State Univ. New York, Syracuse. 306pp.

MAUTZ, W. W., J. KANTER, AND P. J. PEKINS. 1992. Seasonal metabolic rhythms of captive female white-tailed deer: a reexamination. J. Wildl. Manage. 56:656–661.

MOEN, A. N. 1976. Energy conservation by white-tailed deer in the winter. Ecology 57:192–198.

———. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. J. Wildl. Manage. 42:715–738.

MUNDINGER, J. G. 1980. Population ecology and habitat relationships of white-tailed deer in coniferous forest habitat of northwestern Montana. Pages 8–92 *in* Montana deer studies. Job Prog. Rep., Mont. Dep. Fish, Wildl., and Parks, Helena.

NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541–545.

OWENS, T. E. 1981. Movement patterns and determinants of habitat use of white-tailed deer in northern Idaho. M.S. Thesis, Univ. of Idaho, Moscow. 48pp.

OZOGA, J. J., AND L. W. GYSEL. 1972. Response of white-tailed deer to winter weather. J. Wildl. Manage. 36:892–896.

———, AND L. J. VERME. 1970. Winter feeding patterns of penned white-tailed deer. J. Wildl. Manage. 34:431–439.

PARKER, K. L., C. T. ROBBINS, AND T. A. HANLEY. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474–488.

PAULEY, G. R. 1990. Habitat use, food habits, home range, and seasonal migration of white-tailed deer in the Priest River drainage, north Idaho. M.S. Thesis, Univ. of Idaho, Moscow. 153pp.

RAPHAEL, M. G. 1981. Interspecific differences in nesting habitat of sympatric woodpeckers and nuthatches. Pages 142–151 *in* D. E. Capen, ed. The use of multivariate statistics in the studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87.

ROSCOE, J. T., AND J. A. BYARS. 1971. An investigation of the restraints with respect to sample size commonly imposed on the use of the Chi-square statistic. J. Am. Stat. Assoc. 66:755–759.

SAS INSTITUTE INC. 1987. SAS/STAT guide for personal computers. Sixth ed. SAS Inst. Inc., Cary, N.C. 1028pp.

SEAL, U. S., L. J. VERME, J. J. OZOGA, AND A. W. ERICKSON. 1972. Nutritional effects on thyroid activity and blood of white-tailed deer. J. Wildl. Manage. 36:1041–1052.

SILVER, H., N. F. COLOVOS, J. B. HOLTER, AND H. H. HAYES. 1969. Fasting metabolism of white-tailed deer. J. Wildl. Manage. 33:490–498.

SINGER, F. J. 1979. Habitat partitioning and wildlife relationships of cervids in Glacier National Park, Montana. J. Wildl. Manage. 43:437–444.

STAGE, A. R. 1976. An expression for the effect of aspect, slope, and habitat type on tree growth. For. Sci. 22:457–460.

TELFER, E. S. 1970. Winter habitat selection by moose and white-tailed deer. J. Wildl. Manage. 34:553–559.

VERME, L. J. 1965. Swamp conifer deeryards in northern Michigan, their ecology and management. J. For. 63:523–529.

WETZEL, J. F., J. F. WAMBAUGH, AND J. M. PEEK. 1975. Appraisal of white-tailed deer winter habitats in northeastern Minnesota. J. Wildl. Manage. 39:59–66.

WILLIAMS, B. K. 1981. Discriminant analysis in wildlife research: theory and applications. Pages 59–71 *in* D. E. Capen, ed. The use of multivariate statistics in the studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87.

———. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64:1283–1291.

WOODS, G. P. 1984. Habitat selection of white-tailed deer in the Pend d'Oreille Valley, British Columbia. M.S. Thesis, Univ. of Idaho, Moscow. 361pp.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 718pp.

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